

EVOLUTION OF THE STRONGYLOID NEMATODES OF AUSTRALIAN MARSUPIALS

BY

I. BEVERIDGE

There has been a major radiation of members of the nematode order Strongyloidea within the Australian phalangeroid marsupials of the families Macropodidae and Vombatidae, that is the herbivorous kangaroos, wallabies and wombats, with 25 described genera according to a recent classification of the order proposed by Lichtenfels (1980) as well as many undescribed genera (unpublished observations). The strongyloid genera occurring in marsupials have been relatively little studied taxonomically and their phylogeny has consequently been somewhat ignored. This paper therefore proposes a phylogeny of the strongyloid nematodes of marsupials and compares the hypothesis developed with what is known of the phylogeny of the hosts. It concludes that the nematode radiation has been as diverse as that of the hosts and that there are several remarkable examples of convergence in the nematodes, a phenomenon which has been well documented in the hosts.

1. — PHYLOGENETIC RELATIONSHIPS OF THE NEMATODES

The uncertainty of the systematics of these nematodes in the past has made phylogenetic inference difficult. In a major revision of the entire Strongyloidea, Lichtenfels (1980) has provided a workable taxonomic system and has identified characters which are of use in inferring phylogeny. The key features he identified in the ovejector type and the form of branching of the dorsal ray provide the basis for the hypothesis developed below.

The first argument upon which the current hypothesis is based is that all the strongyloid nematodes of marsupials are more closely related to one another than they are to the nematodes of eutherians.

Lichtenfels (1980) by contrast distributed the various genera of nematodes among the subfamilies Cloacininae and Chabertiinae of the family Chabertiidae, and the Phascolostrongylineae and Strongylineae of the family Strongylidae thereby mixing them with nematodes of eutheria and having to postulate a polyphyletic origin for them.

By contrast, it can be argued (though the argument is not developed in detail here) that on the basis of a whole series of male genital characters (bursa, spicules, accessory organs) and cephalic characters, that all are very closely related one to the other and deserve to be grouped within a single taxon. Such a grouping overcomes the exceptions noted by Lichtenfels (1980) to the otherwise close correlation between ovejector type and branching of dorsal ray. Placing emphasis primarily on the ovejector type as he did splits the marsupial strongyloids into several taxa; emphasising the dorsal ray type and other buccal characters as argued here unites them into a single group.

Lineages within the marsupial strongyloids are identified on the basis of the ovejector type as proposed by Lichtenfels (1980); the Type I or Y-shaped ovejector (as defined by Lichtenfels (1980)) is considered "ancestral" along with the presence of a dorsal groove and the externo-dorsal rays

arising from the dorsal ray. All genera of the Cloacininae (Fig. 1) are considered "derived" as they have a Type II or J-shaped ovejector, lack a dorsal groove and have the externo-dorsal rays arising close to the lateral rays. Such an argument leads to the arrangement of taxa as shown in Fig. 1. It requires the assumption that the Type II ovejector evolved independently in two nematode groups.

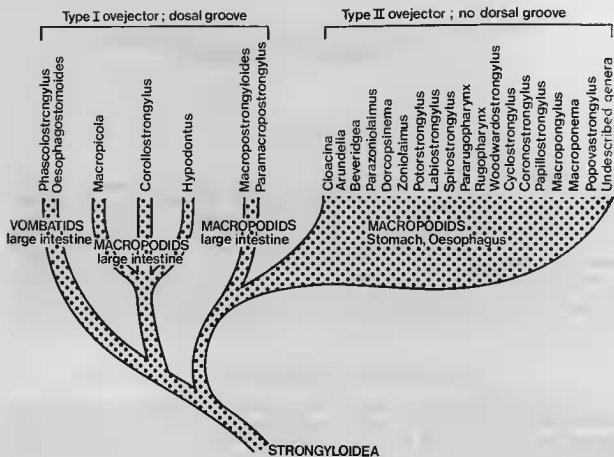


FIG. 1. — Dendrogram of possible phyletic relationships of the Strongyloidea of marsupials.

Two genera are of particular interest. In species of *Macrostrongyloides* and *Paramacrostrongylus*, the buccal capsules are reduced compared with other closely related macropodid inhabiting forms classed as ancestral on the basis of ovejector type and are almost cylindrical, as in genera of the Cloacininae, except that a dorsal gutter is present. The ovejector in some species is a modified Type I, and almost resembles a Type II. They are therefore placed intermediate between the typically "ancestral" genera and the "derived" Cloacininae.

2. — SITE IN HOST

All the so-called "ancestral" genera of nematodes occur in the large intestine of their hosts; *Oesophagostomoides* and *Phascolostrongylus* occur in the colon of wombats; *Macropicola*, *Hypodontus* and *Corollostrongylus* in the caecum, colon and terminal ileum of macropodids; 3 species of *Macrostrongyloides* and 1 species of *Paramacrostrongylus* occur in the caecum; one species of *Macrostrongyloides* and one species of *Paramacrostrongylus* occur in the stomach. As in morphology,

these last two genera occupy an intermediate position between the "ancestral" and "derived" groups of genera as they occur in the two major sites. No marsupial strongyloids occur in the upper small intestine. The 25 genera of Cloacininea occur exclusively in the stomach and œsophagus of the host.

3. — HOST RANGES AND SPECIFICITY

Not all of the major groups of Australian marsupials have strongyloid parasites. None occur in the carnivorous or omnivorous dasyurids and peramelids; all are restricted to the herbivorous Phalangeroidea. Within the Phalangeroidea, strongyloids are absent from the arboreal phalangerids, and occur only in the browsing/grazing vombatids and macropodids.

The "ancestral" genera *Phascolostrongylus* and *Æsophagostomoides* occur exclusively in the colon of wombats, which probably originated in the Eocene (38-55 myrs ago) (Fig. 2). The other "ancestral" genera, (*Macropicola*, *Corollostrongylus*, *Hypodontus*) occur in macropodids and are each represented by a single species, a situation which can best be explained as a series of relicts from an ancient radiation. Each genus differs strikingly from the others, yet each has a subglobular, deviated buccal capsule, a characteristic Y-shaped dorsal groove and Type I ovejector indicating obviously close affinities. *Corollostrongylus* occurs only in *Hypsiprymnodon moschatus*, the single member of the rat-kangaroo sub-family Hypsiprymnodontinae, and the most primitive extant macropodid. *Macropicola* occurs in a very recent host, *Macropus fuliginosus*, but only in a very restricted part of the host's range, again suggesting a relict status. *Hypodontus* is widespread but occurs in both primitive and recent macropodids.

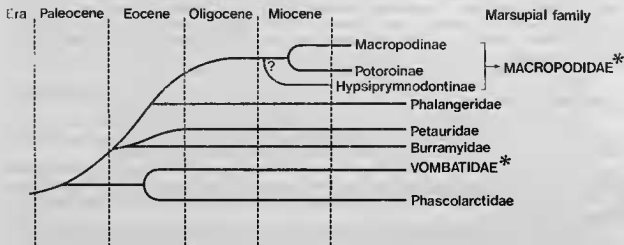


FIG. 2. — Dendrogram of phyletic relationships of the phalangeroid marsupials modified from Stirton *et al.*, 1968 and Kirsch, 1977. Asterisks indicate the marsupial families in which strongyloid nematodes occur.

The 18 genera of the Cloacininae occur in the stomach or œsophagus of marsupials belonging to the family Macropodidae. With the exception of a single genus (*Potorstrongylus*), all genera occur in members of the subfamily Macropodinae which contains the most recently evolved kangaroos and wallabies. Thus, in general nematodes presumed to be ancestral often occur in more primitive hosts; "derived" nematodes occur exclusively in recent hosts.

The radiation of the Cloacininae within the Macropodinae is striking and includes forms inhabiting both the stomach and the œsophagus. Diversity in structure, particularly in the cephalic anatomy occurs along with large numbers of nematodes and large numbers of species occurring in individual host animals. The stomachs of the larger macropodines may contain up to 300,000

nematodes (Beveridge and Arundel, 1979) and the nematode population may consist of up to 6 genera, with up to 10 species of a single nematode genus in an individual host. Two genera, *Cyclostrongylus* and *Spirostrongylus* have invaded the oesophagus of certain species of wallaby and occur coiled around the numerous villi of the papillated oesophagus of the host. Because this distinctive oesophageal morphology occurs in a limited number of macropodine species (*Macropus agilis*, *M. rufogriseus*, *M. dorsalis*, *M. eugenii*, *M. parryi*, *M. parma*, *Wallabia bicolor*) the genera *Cyclostrongylus* and *Spirostrongylus* are limited to these hosts, each host having its own specific parasite. The hosts, with the exception of *W. bicolor* have been placed in a separate subgenus *Priotemnus* by Bartholamai (1975) on morphological grounds and serological evidence supporting this arrangement has been provided by Richardson and McDermid (1978). However, the parasites indicate a close relationship between *Wallabia* and *Priotemnus* which is not shown serologically but which was argued by Sanson (1978) based on dental morphology and function.

By contrast, members of the more primitive rat kangaroo family the Potoroinae (*Potorous*, *Bettongia*, *Epyprymnus*) are either devoid of gastric nematodes or are parasitised by only a single species (genus *Potorostrongylus* with 2 described species). It can be shown that these species have evolved from more primitive members of the Cloacininae and have presumably invaded the Potoroinae from the Macropodinae.

4. — EVOLUTION OF THE STRONGYLOID NEMATODES

The hypothesis put forward therefore is that the ancestors of the strongyloid nematodes of phalangeroids were inhabitants of the large intestines of their hosts. Their browsing hosts (e.g. wombats, *Hypsiprymmodon*) are monogastric, and the pH in the stomach is therefore low.

The primitive nematodes occurred in organs where fermentative digestion occurred and the pH of the content was high. There were ancient radiations of these nematodes presumably at the time of host radiations, with the subsequent extinction of many of the hosts and their nematodes. Major marsupial extinctions seem to have occurred in the Pleistocene (Ride, 1971).

By this means a series of related yet morphologically diverse nematodes (*Esophagostomoides*, *Phascolostrongylus*, *Hypodontus*, *Macropicola*, *Corollostrongylus*) may have evolved.

With the subsequent evolution of the Macropodinae which includes both grazers and browsers a large, highly sacculated fermentative stomach with contents at a high pH developed and therefore opened up new niches which were invaded initially by caecal inhabiting nematodes.

The initial invaders were probably species like *Macropostrongyloides* and *Paramacropostrongylus* which show morphological features somewhat intermediate between the ancestral and derived nematodes and occur in both the caecum and the stomach of macropodids. They then gave rise to the modern cloacinids.

The rapid speciation of the hosts assisted in the enormous diversification now seen in the stomach inhabiting nematodes. For some reason, the Potoroinae, with lesser development of the sacculated stomach were by-passed and have only recently been re-invaded by parasites which evolved in the Macropodinae.

5. — CONCLUSION

The proposed phylogeny of the nematodes (Fig. 1) therefore fits quite well with that of the hosts (Fig. 2). With minor exceptions the genera occurring in vombatids are different to those in macropodids; supposed "ancestral" nematodes occur in known "primitive" or relict hosts; the taxonomic division between the Potoroinae and the Macropodinae is equally clear in the nematode fauna, the latter subfamily having 18 genera of nematodes, the former a single genus.

The Australian marsupials are frequently cited as examples of radiation and convergence in evolution. Remarkable convergences are also apparent in the nematode parasites :

1. the Cloacininae are convergent with the Cyathostominae (strongyles of Perissodactyla) and until recently (Lichtenfels, 1980) were classified with them.
2. *Hypodontus* shows remarkable convergence with the hook-worm sub-family Nectorinae but is in fact a strongyloid.
3. *Esophagostomoides* and *Phascolostrongylus* show convergence with the *Esophagostominae*, in which they were formerly classified.
4. *Corollostrongylus* is superficially similar to the genus *Custorstrongylus*, a parasite of beavers in North America.
5. *Cyclostrongylus*, *Spirostrongylus* have developed attachment mechanisms similar to certain trichostrongyloids.

The presence of the Strongyloidea in two of the more recently evolved (diprotodont) marsupial families, and not in the more primitive polyprotodont families, together with the fact that the diprotodont families evolved after the separation of the Australian continent from Antarctica suggests that the herbivorous marsupials acquired these parasites from other animals already present in Australia. Genera of the Strongyloidea occur in mammals, with the exception of *Syngamus* in birds, two genera in tortoises and three genera in ratite birds. The last mentioned association is interesting since ratites are known to be primitive, have a Gondwanaland distribution and occur in Australia. Furthermore, the genera in ratites, particularly *Codiostomum* in ostriches, are similar in many respects to the ancestral strongyloid genera in Australian marsupials. It may be therefore that we should look for the precursors of the Australian strongyloids in the large intestines of Australian ratites.

The conclusions presented here indicate that superficial comparisons between the strongyloids of marsupials and eutherians may require re-assessment. There is no need to believe, as Cameron (1964) did, that the kangaroos were in contact with primitive ungulates in Africa, probably during the Pleistocene. Rather, the kangaroos evolved in Australia well after its separation from the other continents and the isolation and radiation of nematodes within the Australian fauna has now produced forms that are convergent with but phylogenetically distinct from strongyloids in ungulates.

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DISCUSSION

- ANDERSON. — What are the implications of your remarks for the modern classification of the Strongyloidea proposed by Dr. Lichtenfels ?
- BEVERIDGE. — First of all, I am quite unstinting in my praise for the Lichtenfels key. It seems to me that for the first time one can make some sense of the Strongyloidea, and particularly the relationships of the Australian Strongyloidea. It is in fact the classification of Lichtenfels which stimulated the present attempt at a hypothesis for the origins of the Strongyles of Marsupials. Having said that, if the hypothesis presented above is correct, thence the classification of Lichtenfels requires modification. At present however, it is only a hypothesis which needs to be tested further before it is incorporated into a classification. These are yet many genera to describe and tribes to revise, and I think this must be done before the higher classification is constructed. In brief, I think that improvements can be made to Lichtenfels classification, but it is too early at present.
- SCHAD. — Are the sacculations of the stomach of kangaroos constant in number and identifiable from one individual to another, in a given species ? If so, how are the numerous species of Strongyles distributed in these divisions of the stomach ? And, finally, if the taxonomy is sufficiently definitive, what can be said about interspecific competition ?
- BEVERIDGE. — The sacculations are constant within a species, but differences between species are marked, ranging from the simple monogastric stomach in *Hypsiprymmodon*, to the tubular, partially sacculated stomach of the Potoroinae, and then the complex sacculated stomachs of the Macropodinae. Work on the distribution of Strongyles in the stomach thus far has been very superficial, but enough has been done to show that certain genera occur principally in one or other region of the stomach. The most interesting genus is definitely *Cloacina* where up to 12 species of the same genus may occur in the stomach of a single animal. However many of the species of the genus are undescribed, and at present work on interspecific competition would be very difficult indeed.
- CHABAUD. — Je suis d'accord avec Mr Beveridge pour son hypothèse sur l'origine des Strongles australiens à partir des Strongles de Ratites.
Mais le genre *Sauricola* chez les tortues n'offre-t-il pas une autre possibilité ?
- BEVERIDGE. — Il n'y a pas de tortues terrestres en Australie.
- LAVOCAT. — Peut-être sont-elles éteintes ?
- BEVERIDGE. — C'est tout à fait possible.
- FAIN. — A propos du polyparasitisme par un même genre, nous avons trouvé chez *Potorous* 21 espèces d'un même sous-genre. Pourquoi spécialement chez cet hôte ? *Potorous* est-il un fossile vivant ?
- BEVERIDGE. — Non, il existe à la fois en Tasmanie et aussi sur le continent.
- LAVOCAT. — Avez-vous réellement affaire à des espèces différentes ?
- FAIN. — Oui, certainement.
- SCHAD. — Actually, the co-occurrence of numerous closely related species of Nematodes in individuals of a host species occurs quite often. For example, in the large intestine of herbivorous tortoises, in the large intestine of the horse, etc... It is frequently associated with voluminous habitats specialized for cellulose digestion where there are diverse micro-organisms upon which Nematodes can feed differentially.
- CHABAUD. — Ce problème est un des nouveaux sujets intéressants de la parasitologie. Depuis les travaux de Schad et de Petter sur les Oxyures du colon des Tortues, le phénomène du polyparasitisme par des espèces congénériques a été observé même chez des animaux dépourvus d'un gros intestin. Si le temps nous en offre la possibilité, il faudra revenir sur ces problèmes le dernier jour du Colloque.